

DISTRIBUTION AND FEEDING OF THE HORSESHOE CRAB, *LIMULUS POLYPHEMUS*, ON THE CONTINENTAL SHELF OFF NEW JERSEY¹

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ABSTRACT

The horseshoe crab, *Limulus polyphemus*, population was assessed during hydraulic dredge surveys of the surf clam resource in the inshore 5.5 km (3 nautical miles) of the continental shelf off New Jersey from 1976 through 1979. Frequency of occurrence and abundance was higher off the southern half of the state, which may be a function of its proximity to Delaware Bay, a principal spawning site. Horseshoe crabs consumed various benthic organisms, primarily bivalves, arthropods, and polychaetes. Surf clams, *Spisula solidissima*, were important in the diet of *Limulus*; individual valves ranged in length from <1 mm to about 35 mm. In the laboratory, horseshoe crab predation was observed on surf clams as long as 46 mm.

This report describes the distribution of the horseshoe crab, *Limulus polyphemus*, on the inshore continental shelf off New Jersey, and the diets of a sample of these animals. Previous studies of the horseshoe crab on the continental shelf are limited to distributional records (Wolff 1977; Shuster 1979) or tagging studies conducted close to estuarine spawning areas (Baptist et al. 1957; Rudloe 1980), although crabs have been found at depths as great as 200 m according to National Marine Fisheries Service surveys (J. W. Ropes⁴).

Since the early 1960's, an intensive surf clam, *Spisula solidissima*, fishery has developed along the New Jersey coast (Ropes 1982). The junior author (Haskin) and his colleagues have inventoried the surf clam resource in the New Jersey waters, to 5.5 km (3 nmi) offshore yearly since 1972. All macroinvertebrates, including *L. polyphemus*, captured in hydraulic dredge hauls from 1976 through 1979 were counted. Since a percentage of the horseshoe crab population migrates from the continental shelf to estuaries and back again (Shuster 1982), we analyzed both tem-

poral and spatial variability. Separating these effects was difficult because the sampling program was designed primarily to inventory a sessile clam resource, rather than a migratory one. However, the data, based on over 1,100 stations, still represent the most systematic survey of *L. polyphemus* distribution on the inshore continental shelf, and since exploitation of these crabs for biomedical research and bait is increasing (Pearson and Weary 1980), our study provides baseline information should future population assessment studies be warranted.

Information on the feeding biology of horseshoe crabs is limited (Lockwood 1870; Fowler 1908; Shuster 1950; Smith and Chin 1951; Smith 1953; Smith et al. 1955; Botton 1981). In this study, stomach contents from 36 horseshoe crabs from the continental shelf were examined to supplement a more intensive study of the food habits of animals from Delaware Bay (Botton 1982); in August 1980, predation by crabs on surf clams about 4 cm long was examined in the laboratory.

MATERIALS AND METHODS

Population Survey

Stations were sampled with a hydraulic dredge (Meyer et al. 1981), adjusted to retain surf clams >88 mm. This gear retained both adult and sub-adult horseshoe crabs. Catch data, as number of animals per tow, were normalized for dredge width and tow time. The standard tow (ST) is defined as a 5-min haul using a 152 cm knife (width of dredge).

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⁴J. W. Ropes, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun. February 1983.

This standard tow covered an area of about 418 m².

The New Jersey coastline from Cape May to Shark River Inlet was subdivided into 19 areas (Table 1). Stations were located by 3-point sextant fixes and/or loran C, and grouped in intervals of 0-1.8 km (0-1 nmi) (0-0.9 and 0.9-1.8 km north of Beach Haven Inlet), 1.8-3.7 km (1-2 nmi) and 3.7-5.5 km (2-3 nmi) based on distance from land. Inlets were used as latitudinal break points (Fig. 1). Because of the reduced sampling effort from 1.8 km offshore, these areas were larger than areas inshore of 1.8 km.

For statistical analysis, all tows on the same day in a given area were considered replicates. The Analysis of Variance (ANOVA) for the number of crabs per tow had three sources of variation: Area, time nested within area, and replicate tow nested within time within area. Because each year's design was unbalanced, a pseudo-F procedure (Hicks 1973) tested the significance of the area effect. Data were log-transformed to stabilize the variances. When areas were sampled more than once in a given year, we tested differences between sample dates using a completely randomized one-way classification ANOVA. If the F-test was significant, a Student-Neumann-Keuls procedure for unequal group sizes tested for differences between the means for each sample date (Zar 1974).

TABLE 1.—Description of areas of the New Jersey coast surveyed from 1976 to 1979.

Distance offshore (km)	Area	Southern boundary	Northern boundary
0-1.8	1	Cape May Inlet	Hereford Inlet
	2	Hereford Inlet	Stone Harbor
	3	Stone Harbor	Townsend Inlet
	4	Townsend Inlet	Corson Inlet
	5	Corson Inlet	Great Egg Harbor Inlet
	6	Great Egg Harbor Inlet	Absecon Inlet
	7	Absecon Inlet	Beach Haven Inlet
	8	Beach Haven Inlet ¹	Barnegat Inlet
	9	Beach Haven Inlet ²	Barnegat Inlet
	10	Barnegat Inlet	Shark River Inlet
	11	Barnegat Inlet ²	Shark River Inlet
1.8-3.7	12	Cape May Inlet	Townsend Inlet
	13	Townsend Inlet	Absecon Inlet
	14	Absecon Inlet	Beach Haven Inlet
	15	Beach Haven Inlet	Shark River Inlet
3.7-5.5	16	Cape May Inlet	Townsend Inlet
	17	Townsend Inlet	Absecon Inlet
	18	Absecon Inlet	Beach Haven Inlet
	19	Beach Haven Inlet	Shark River Inlet

¹0-0.9 km.
²0.9-1.8 km.

Stomach Contents

Thirty-six adult *L. polyphemus* were collected between 10 July and 25 August 1978 for analysis of

stomach contents. The results are grouped for three locations: Stone Harbor (1 station, 5 individuals), Atlantic City (12 stations, 24 individuals), and Point Pleasant (3 stations, 7 individuals) (Fig. 1).

Complete digestive tracts were removed from crabs aboard ship or shortly after returning to the laboratory, fixed in 10% Formalin⁵ seawater, and later transferred into 70% ethanol until examination. Food, much of which was entangled with mucus, was sorted under a 10× stereoscope. The number of bivalves was determined by counting the number of umbones and dividing by 2. Shells were measured by ocular micrometer or vernier caliper.

RESULTS

Population Surveys

1976 Survey

Sampling commenced in mid-July and was most extensive in late August and early September; no areas north of Beach Haven Inlet were sampled. Horseshoe crabs were present in over 90% of all hauls in the first 1.8 km between Hereford Inlet and Townsends Inlet, and from 1.8 to 3.7 km between Cape May and Townsends Inlet (Table 2). More than 10 animals/ST were dredged from 1.8 to 3.7 km offshore between Cape May and Absecon

⁵Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—1976 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	N stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	27	85.2	7.7	0.81	25.7
	2	12	66.7	4.1	1.27	10.7
	3	21	90.5	6.0	0.65	15.0
	4	7	71.4	11.2	1.14	35.3
	5	9	88.9	4.8	1.05	15.0
	6	8	62.5	2.4	1.01	5.4
1.8-3.7 km	7	10	70.0	7.2	1.01	20.0
	12	31	90.3	14.6	0.69	47.1
	13	28	78.6	12.5	2.36	145.7
3.7-5.5 km	14	10	80.0	3.0	0.88	6.0
	16	18	83.3	6.6	0.97	26.8
	17	16	62.5	25.4	2.72	277.4
	18	7	42.9	1.1	1.30	3.2
	19	7	42.9	1.1	1.30	3.2

Analysis of Variance:

Source	df	SS	MS	F	P
Total	202	259.94			
Area	12	40.08	3.34	1.12	ns
Time (area)	38	80.77	2.13	2.32	0.05
Station (time (area))	152	139.09	0.92		

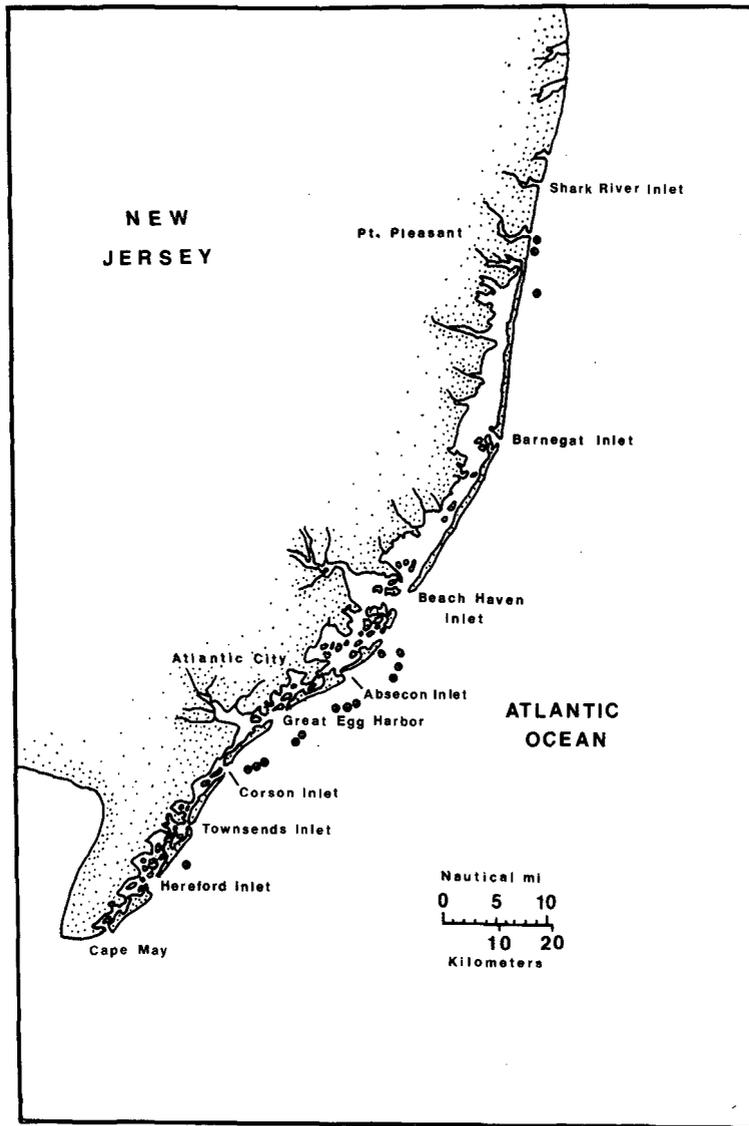


FIGURE 1.—Map of the New Jersey coast. Filled circles show the locations of stations from which *Limulus polyphemus* stomach contents were obtained.

Inlets, and in several areas from 0 to 1.8 km and 3.7 to 5.5 km between these two inlets. Two hundred seventy-seven crabs were found in a single dredge tow, 5.4 km off Townsends Inlet.

In 1976, both time within area and station within time within area were greater sources of variability than area itself (Table 2). The inshore 1.8 km from Cape May to Hereford Inlets was sampled on 10 and 30 July and again on 4-5 September. The mean number of crabs collected per standard tow on each date was 8.3, 9.3, and 2.1, respectively

($F = 2.86, 0.10 < P < 0.05$). There were no significant differences between sampling dates within any other individual areas.

1977 Survey

Most sampling in southern New Jersey was done in June and July, but the areas north of Beach Haven Inlet were sampled in August. Thus, temporal variability was confounded with geographic variability. Areas north of Beach Haven Inlet were

relatively depauperate; the area effect was significant at $P < 0.07$ (ANOVA); the time within area effect was significant at $P < 0.05$ (Table 3).

Limulus polyphemus occurred in 70% to 100% of all tows between Cape May and Absecon Inlet (Table 3). Crabs were most numerous from 0 to 1.8 km offshore between Cape May and Hereford Inlets. When sampled on 15 June (23 stations), there was an average of 15.52 crabs/ST, but in late August-early September (9 stations), only 2.17 crabs/ST ($F = 5.006, P < 0.05$). Abundance from 1.8 to 3.7 km between Cape May and Townsends Inlets declined over the same time, from 13.08 to 3.3 crabs/ST ($F = 4.805, P < 0.05$). From 1.8 to 3.7 km offshore, between Townsends Inlet and Absecon Inlet, crabs declined between early July ($\bar{x} = 25.33, n = 6$), late July-early August ($\bar{x} = 3.95, n = 14$), and late August ($\bar{x} = 7.6, n = 5$), but the differences were marginally significant ($F = 3.03, 0.10 < P < 0.05$).

Horseshoe crabs were encountered in every tow in the first 1.8 km from Beach Haven Inlet to Barnegat Inlet, although the average abundance was only 5 crabs/ST. No other area north of Atlantic City contained over 4 crabs/ST and an onshore-offshore gradient was particularly evident between Beach Haven Inlet and Shark River Inlet.

TABLE 3.—1977 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	N stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	34	94.1	11.3	1.41	87.0
	2	10	70.0	2.8	1.29	12.0
	3	16	93.8	7.0	0.83	20.6
	4	17	100.0	6.1	0.68	14.2
	5	8	100.0	5.9	0.64	12.0
	6	8	75.0	2.9	0.89	7.0
	7	8	75.0	2.0	0.82	4.0
	8	12	100.0	6.0	0.79	19.6
	9	4	100.0	4.4	0.28	6.0
	10	25	60.0	2.2	1.62	13.9
1.8-3.7 km	11	4	75.0	2.6	1.22	7.1
	12	25	84.0	5.5	1.61	44.0
	13	25	92.0	9.8	1.96	97.0
	14	7	100.0	4.1	0.79	10.0
3.7-5.5 km	15A ¹	9	44.0	1.6	1.34	5.4
	15B ²	6	33.3	0.9	1.93	4.3
	16	26	96.1	9.6	0.76	22.4
	17	9	77.8	7.6	1.44	33.0
	18	9	44.4	3.0	1.82	16.6
	19	7	0.0	0.0	—	0.0
Analysis of Variance:						
Source	df	SS	MS	F	P	
Total	261	258.36				
Area	19	76.05	4.00	1.79	0.07	
Time (area)	32	50.07	1.56	2.48	0.05	
Station (time (area))	210	132.23	0.63			

¹Beach Haven Inlet to Barnegat Inlet.

²Barnegat Inlet to Shark River Inlet.

From 1.8 to 3.7 km offshore, crabs were found in only 40% of the tows, and from 3.7 to 5.5 km, no crabs were present at seven stations.

1978 Survey

As in 1977, the areas north of Beach Haven Inlet were sampled late in the summer. Stations south of Atlantic City had many more horseshoe crabs than ones farther north, and from Beach Haven Inlet northward, few animals were encountered offshore of 1.8 km (Table 4). Area and time within area effects were significant (ANOVA, $P < 0.01$; Table 4).

Temporal variability within an area was difficult to analyze, because for most areas, either the survey was completed in a single weekend, there were low densities on all dates (north of Beach Haven), or there were small sample sizes on one or more cruises. Between Cape May and Townsends Inlet, from 3.7 to 5.5 km offshore, there were significantly more crabs on 20 July ($\bar{x} = 12.64, n = 11$) than on 24 June ($\bar{x} = 3.11, n = 9$) ($F = 26.998, P < 0.001$).

1979 Survey

In contrast to 1977 and 1978, sampling of the Beach Haven Inlet to Shark River Inlet region

TABLE 4.—1978 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	N stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	32	96.9	16.7	0.79	54.0
	2	10	90.0	12.2	0.71	24.0
	3	21	90.5	10.4	0.70	28.0
	4	14	100.0	13.4	0.46	24.0
	5	10	100.0	4.0	0.64	8.0
	6	14	50.0	2.4	2.19	20.0
	7	22	54.5	0.8	1.47	5.2
	8	13	46.2	0.9	1.28	3.0
	9	11	72.7	3.6	0.94	9.0
	10	25	64.0	2.2	1.05	6.4
1.8-3.7 km	11	8	37.5	1.9	2.18	11.8
	12	15	86.7	13.7	2.67	150.0
	13	20	85.0	3.5	1.26	20.0
	14	12	58.3	1.2	1.26	5.0
3.7-5.5 km	15	12	41.7	1.0	1.90	6.4
	16	20	90.0	8.4	0.75	20.0
	17	13	84.6	3.3	0.74	7.0
	18	9	55.6	2.3	1.56	11.0
	19	5	0.0	0.0	—	0.0
Analysis of Variance:						
Source	df	SS	MS	F	P	
Total	281	347.91				
Area	18	165.30	9.18	4.38	0.01	
Time (area)	35	38.72	1.11	1.76	0.01	
Station (time (area))	228	143.89	0.63			

took place early in the summer, thus enabling a comparison of the southern and northern parts of the coast without a confounding effect of time. Both area (ANOVA, $P < 0.01$) and time ($P < 0.01$) effects were significant, and percent occurrence and abundance were low from Beach Haven Inlet northward, where horseshoe crabs were particularly scarce offshore of 1.8 km (Table 5). The inner 0.9 km from Barnegat Inlet to Shark River Inlet had significantly more *L. polyphemus* on 24 June ($\bar{x} = 5.48, n = 12$) than 17 August ($\bar{x} = 0.07, n = 10$) ($F = 11.913, P < 0.005$). From 3.7 to 5.5 km offshore between Townsends Inlet and Absecon Inlet, the density in late July ($\bar{x} = 3.24, n = 8$) was significantly higher than the density found on 17 May or 26 June ($\bar{x} = 0.88, n = 6$ and $\bar{x} = 1.4, n = 3$, respectively) ($F = 6.646, P < 0.005$). Stations on 28 August and 16 November, also contained fewer crabs ($\bar{x} = 0.19, n = 4$ and $\bar{x} = 0.44, n = 2$, respectively).

Stomach Contents

Stone Harbor individuals were collected on 24 July 1978, from a station, 13.4 m depth and 3.7 km offshore, which contained 150 *L. polyphemus*. Their digestive tracts were packed ($\bar{x} = 383.2$, range 88-791 individuals/crab) with blue mussels, *Mytilus edulis*; there were only traces of other food

(three other bivalves, four brachyuran crabs, two foraminifera, and polychaete setae). The mean length of 38 whole valves was 6.3 mm, with a range from 4.2 to 9.0 mm. Virtually all remaining umbones were estimated to be from mussels in that range.

Crabs in the Atlantic City series ate a variety of food, primarily bivalves, annelids, and arthropods (Table 6). The surf clam, *Spisula solidissima*, was an important prey item, ranking first in frequency of occurrence and third in total abundance. Valves <1 mm in length were found, as were portions of a 35-40 mm shell length individual; about 62% of the valves were >4 mm. Other important bivalves were *Tellina* sp. and *Siliqua costata*. Twelve polychaete taxa were identified, of which *Nereis* sp. was the most frequently occurring, while the most abundant were unidentified Spionidae. Fifteen digestive tracts contained one or more specimens of brachyuran crabs, which in several cases were identified as young rock crabs, *Cancer irroratus*.

Stomachs of the seven horseshoe crabs from the Point Pleasant series contained little food. Only four bivalves (one *S. solidissima* and three *M. edulis*), a gastropod (*Nassarius trivittatus*), and a brachyuran were identified. Polychaete setae were

TABLE 5.—1979 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	N stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	30	96.7	20.2	1.20	107.8
	2	11	100.0	9.6	0.70	18.3
	3	21	100.0	15.5	0.63	33.3
	4	20	100.0	20.6	0.96	92.5
	5	9	100.0	9.4	0.67	19.2
	6	19	68.4	3.8	1.13	14.2
	7	20	55.0	1.4	1.15	5.1
	8	20	55.0	1.7	1.38	7.5
	9	11	63.6	2.0	1.49	10.3
	10	22	45.5	3.0	1.50	13.3
	11	4	25.0	0.2	2.00	0.7
1.8-3.7 km	12	23	95.7	7.9	1.25	41.7
	13	20	70.0	2.9	1.92	25.0
	14	19	73.7	2.4	0.94	8.3
	15	8	50.0	1.5	1.48	5.1
3.7-5.5 km	16	15	100.0	7.8	1.05	32.5
	17	26	73.1	2.6	1.55	20.0
	18	16	43.8	1.3	1.52	6.2
	19	3	0.0	0.0	—	0.0
Analysis of Variance:						
Source	df	SS	MS	F	P	
Total	312	401.42				
Area	18	206.37	11.46	4.74	0.01	
Time (area)	47	62.30	1.33	2.46	0.01	
Station (time (area))	247	132.76	0.54			

TABLE 6.—Ranking of food items by total abundance and frequency of occurrence, from 24 *Limulus polyphemus* collected in the Atlantic City series, summer 1978.

Item	Number of specimens	Rank	Number of occurrences	Rank
Foraminifera	136	1	9	5
Unidentified bivalve	65	2	13	2
Spisula	48	3	14	1
Tellina	42	4	10	4
Brachyura	16	5	11	3
Siliqua	16	5	6	6
Spionidae	15	6	3	9
Nematoda	10	7	4	8
Cancer	9	8	4	8
Fecal pellets	9	8	9	5
Plant material	9	8	9	5
Gemma	8	9	5	7
Glycera	7	10	3	9
Polychaete setae	6	11	6	6
Ensis	6	11	5	7
Polynoidae	6	11	3	9
Mytilus	4	12	4	8
Nereis	4	12	4	8
Cirripedia	3	13	3	9
Spiophanes	3	13	2	10
Ampharetidae	2	14	2	1
Anomia	2	14	2	10
Capitellidae	2	14	2	10
Isopoda	2	14	2	10
Mulinia	2	14	2	10
Nemertea	2	14	2	10
Ostracoda	2	14	2	10
Turbellaria	2	14	2	10
Unidentified gastropod	2	14	2	10
Unidentified oligochaete	2	14	1	11
(Tie-17 items)	1	15	1	11

noted in two samples and unidentified shells in three. The most numerous item was Foraminifera ($n = 21$), and no other item was found more than three times.

In a laboratory experiment, a 20.3 cm (prosomal width) male horseshoe crab ate one 40.6 mm surf clam; the same crab consumed two clams, 43.8 and 42.4 mm, several days later (see Botton 1982 for procedural details). A 27.9 cm female ate two clams, 46.0 and 36.2 mm. Clams of this size are manipulated by the walking legs so that the ventral shell margin is held against the gnathobases. The chitinous gnathobases chip the ventral margin, eventually resulting in the fracture of one of the valves. Cracking of the valves continues until the crab is able to remove the meat from the shell using the pincer-tipped walking legs or the chelicerae. Ingestion of the shell of 4 cm *S. solidissima* is apparently incidental.

DISCUSSION

A latitudinal gradient in horseshoe crab abundance along the New Jersey coast during the spring and summer months was recognized as a decrease in abundance with distance north from Delaware Bay, and an onshore-offshore gradient was apparent in northern New Jersey. The transition between areas of high and low density takes place between Great Egg Harbor Inlet (Ocean City) and Absecon Inlet (Atlantic City). Horseshoe crabs were more abundant inshore in the late spring and early summer than in the late summer and fall.

Why are adult *L. polyphemus* concentrated in southern New Jersey, at least during the spring and summer? Since Delaware Bay, in southern New Jersey, contains the largest spawning population of horseshoe crabs in North America (Shuster 1982), we believe that the distribution on the New Jersey continental shelf may be related to the migration of deep-water crabs to those beaches for reproduction. However, horseshoe crabs spawn elsewhere in New Jersey and are widely distributed on the middle Atlantic continental shelf (Shuster 1979); based on electrophoretic evidence (Selander et al. 1970), there is gene flow between widely separated populations.

Hydraulic surf clam dredges are efficient samplers of large benthic infauna (Meyer et al. 1981), but an evaluation of this dredge as a means of capturing *L. polyphemus* is lacking. Given its sluggish habits, it is unlikely that gear avoidance

by horseshoe crabs significantly affects our results; indeed, much more active lady crabs, *Ovalipes ocellatus*, are caught in large numbers (Meyer et al. 1981; Haskin, unpubl. data). However, in the absence of direct observations, it is perhaps best to consider our results as relative, rather than absolute abundances of horseshoe crabs off New Jersey. Because the temporal sequence of sampling varied yearly and because the effect of time on abundance was statistically significant, we do not encourage speculation on year-to-year variability based on these data.

The horseshoe crab is a dietary generalist; based on the limited number of animals dissected, molluscs, arthropods, and polychaetes are the major food items. Although Foraminifera were numerous, they are probably ingested inadvertently while digging out infauna. Opportunistic foraging was shown from the Stone Harbor group, which fed almost exclusively on *M. edulis*. Smith (1953) noted that crabs could locate discrete patches of soft-shell clam, *Mya arenaria*, but the behavioral basis for patch selection is unknown.

Horseshoe crab predation may be an important source of juvenile surf clam mortality. In aquaria, crabs ingested only the meats of 4 cm *S. solidissima*; this implies that this species may be more important as food than is apparent from visual stomach content analysis, which relies heavily on shell remains. Young *S. solidissima* may have been underestimated because many small (0.5-2.0 mm) shells were categorized only as "unidentified bivalves." Further studies of the food habits of horseshoe crabs, and of the abundance and diets of other predators, are necessary to evaluate the importance of predation in the survivorship of juvenile surf clams in New Jersey.

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